Mesozooplankton trends and distributions in pelagic and littoral habitats of the Archipelago Sea, the northern Baltic Sea, SW Finland

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This study investigated the occurrence and diversity of zooplankton communities in the Archipelago Sea, the northern Baltic Sea, SW Finland. Zooplankton was sampled from rocky shores in three regions: the inner archipelago (at Paimionlahti), the middle archipelago (at Seili), and the outer archipelago (at Utö) in autumn 1997. Samples were taken from the surface layer (0–1 m) in the coastal zone, i.e., in the littoral and in the nearby pelagic areas during the day and during the night. Zooplankton taxa were identified for groups of cladocerans (*Cladocera*), copepods (*Copepoda*), or rotifers (*Rotifera*). We investigated whether the archipelago zonation is observable also in the distribution of zooplankton communities, mainly on the basis of species numbers, abundances, the Shannon-Wiener (H') and the Simpson Diversity (D) Indices, and whether there are differences in species numbers and diversity between the day and the night (through vertical migration) or between the littoral and the pelagic habitats. Comparisons were made with non-parametric ANOVA and generalized linear models (GENMOD). Analyses revealed that the archipelago zones can, to a certain extent, be observed on the basis of the numbers of zooplankton species. Species numbers and diversity generally increased towards the outer archipelago in both the littoral and the pelagic habitats. The increase can be explained mainly by the seawater salinity. Zooplankton diversities between the day and night and between the littoral and the pelagic habitats were different in the inner and outer archipelagos that can be explained by zooplankton horizontal and vertical migrations or drifting. The results are discussed considering the zooplankton community changes that have occurred in the study area since 2000.

Introduction

In the Baltic Sea area, the discussion of the changes in the marine environment is mainly focused on two main subjects, i.e., eutrophication and climate change. Increasing eutrophication has been a concern especially for the Baltic Marine Environmental Protection Commission (e.g., HELCOM 1996), while climatic drivers have drawn scientific attention to the ecological status and

the future of the Baltic Sea (e.g., Hänninen et al. 2000a, Schrum 2001, Conley et al. 2002, Hänninen et al. 2003). Changes in environmental factors in the Baltic Sea are complicated, because they occur in an extensive system of gradients formed in the N-S dimension of the sea due to the discharge of numerous rivers (Voipio 1982).

For a long time, seawater salinity has been considered to be the most important controller of the Baltic Sea biodiversity (Kändler 1949, Hela

1951, Purasjoki 1958), as the mechanism behind it is most likely the osmotic stress caused for the fauna and flora. The Baltic Sea zooplankton species composition and abundance have been repeatedly shown to depend on changes in salinity, originally presented by Segerstråle (1969). Since then, climatic factors in the Atlantic Ocean have been seen as a basic controlling factor not only in the hydrography (i.e., salinity and temperature; Hänninen 2022), but ultimately also in the zooplankton of the Baltic Sea (Vuorinen et al. 1998, Hänninen et al. 2000a, 2003, Vuorinen et al. 2003). Additionally, the importance of salinity as a zooplankton composition regulator has been reported in different regions of the Baltic Sea, e.g., Ojaveer et al. 1998, Vuorinen et al. 1998, Möllmann & Köster 1999, Dippner et al. 2000, Möllmann et al. 2000, Kornilovs et al. 2001, Hänninen et al. 2003, Vuorinen et al. 2003, and Mäkinen et al. 2017. A review of these publications reveals the increasing interest in selective planktivory as an alternative explanation or a contributor to salinity-induced changes in zooplankton (Hänninen et al. 2000a, Möllmann 2001, Mäkinen et al. 2017).

Daily vertical migration of zooplankton is a common global phenomenon among plankton communities. It has been known for over 100 years, observed practically in all zooplankton taxa (Clarke 1934), and it has been considered to be the biggest contemporary migration of fauna biomass during one day (Vuorinen 1986). Globally, the average migration distance traveled in the marine environment has been estimated to be 100–400 meters per day (Nybakken 1997). Migration is mainly caused by the daily variation in the daylight (Ackefors 1969, Nybakken 1997). Vuorinen (1986) has suggested that no single reason can explain vertical migration, instead, it is the result of a combination of several factors. Horizontal zooplankton migration has not received as much scientific attention as the vertical one. However, as zooplankton distribution occurs mainly in patches, it thus can be considered to be largely caused by the same reasons as vertical migration (Sandström 1979).

Mesozooplankton is defined as the 200–2 000 µm size fractions of a zooplankton community (Hernroth 1985). In this study, we concentrated only on the three most representative taxa in this size class found in the brackish water of the coastal area of Finland, i.e., the phylym Rotifera (i. e., rotifers), the suborder Cladocera (i.e., water fleas or cladocerans), the subclass Copepoda (i.e., copepods), and the most common species of the studied taxa. Zooplankton studies in Finnish coastal waters has a long history (e.g., Levander 1900, Leegaard 1920, Segerstråle 1969). However, there is only little information on the regional distribution of zooplankton (Viljamaa 1985, Kankaala 1987, Vuorinen & Ranta 1987, Viitasalo et al. 1990, Viitasalo 1992, Vuorinen et al. 2003).

The purpose of this work was to study zooplankton community structures in three different areas in the Archipelago Sea, northern Baltic Sea. The study aimed to determine whether there are differences in zooplankton community structures, species composition, or diversity indices calculated on the basis of species numbers between the zones of the inner, middle, and outer archipelagos. The study investigates differences in the occurrence of zooplankton species between the shallow littoral and pelagial water (i. e., horizontal migration), as the littoral zone close to the shore forms a significant breeding, spawning, feeding, and protective place for most aquatic organisms (Leppäkoski et al. 1999, Hänninen et al. 2007). Correspondingly, we aimed to reveal whether there are differences in species distributions during the daytime and during the nighttime (i.e., vertical migration) within littoral and pelagic areas. As the sampling of the present study was conducted already at autumn 1997, the results are discussed in view of the zooplankton community changes that have occurred in the study area since 2000 (Mäkinen et al. 2017).

Materials and methods

Study area

The Archipelago Sea is a semi-enclosed archipelago at the southwest coast of Finland between the Baltic proper and the Bothnian Sea (59°45'–60°45'N and 21°00'–23°00'E) in the northern Baltic Sea (Fig. 1). Depending on the definition of an island, the area is estimated to contain up to 60 000 islands, of which some 41 000 are named in regional charts (Väänänen et al. 2020). In this respect, it is the biggest archipelago in the world.

It has a complex and variable bathymetry and mainly wind-driven water mass movement patterns.

The basement of the Archipelago Sea is composed of a ragged half-plateau, or peneplain, created by prehistoric tectonic upheavals. Fractures and transition lines of the earth's crust are typical in a seabed, where the sea is deeper than elsewhere (Jumppanen & Mattila 1994, Kirkkala 1998). The special topographical characteristic of the Archipelago Sea is its zonation in accordance with the relative shares in the land or seascape areas. Originally Häyrén (1900), by using this biogeographical criterion, divided the archipelago into three zones. He showed that zonation ranges from the sheltered inner archipelago, where the landscape dominates, to the middle zone (even proportions), and finally to the more open, seascape dominating, outer archipelago. The existence of these zones is caused by the slow postglacial uplift of the tilting coastal plain, around 0.5 cm annually, and this uplift has been estimated to proceed some 10 000 years, still (Johansson et al. 2002). Hänninen et al. (2000b) proved that zonation could also be traced in water quality, i.e., in the nutrient concentrations in seawater that form a hydrographical zonation comparable to those found in biogeographic studies. The total area of this brackish water sea is 9 436 km^2 with

a water volume of 213 km^3, and the salinity of seawater increases from the inner archipelago towards the outer islands from 4.5 to 6.5 PSU (Voipio 1981, Kirkkala et al. 1998). The total catchment area of the Archipelago Sea is approximately 8 900 km^2 with a lake area of less than 2% and arable land 28% (Hänninen et al. 2000b).

River runoffs from the mainland usually discharge into a shallow bay where the freshwater mixes with seawater slowly. Due to the counterclockwise water circulation in the Baltic Sea, caused by the natural Coriolis effect, the Archipelago Sea is considered to be as a flow-through area through which surface waters from the Baltic Sea and the Gulf of Finland flow into the Bothnian Sea (Jumppanen & Mattila 1994, Kirkkala et al. 1998). The average water depth of the Archipelago Sea is only 23 meters, as the deepest hollows reach 140 meters. The wind-caused sea level variation is generally low with mostly ± 0.5 meters variation compared to the theoretical mean level with the insignificant tidal fluctuation (BACC 2008). The sea stratifies during summer, with a metalimnion or thermocline developing between 15 and 20 meters. The sea is characterized by strong seasonality with the summer temperature of seawater reaching 20 °C and with 0–60 days of ice cover during the winter (Leppäranta & Myrberg 2009).
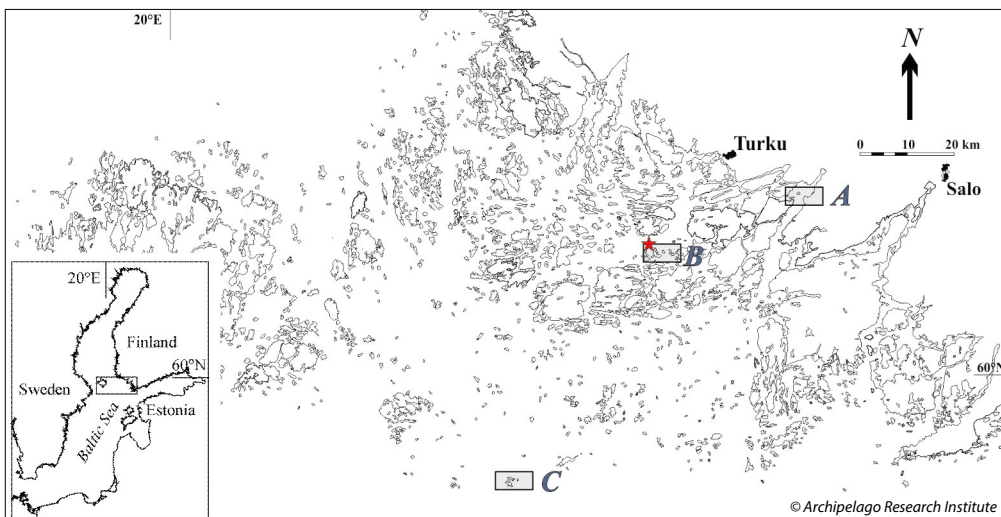

Figure 1. Studied locations in the Archipelago Sea. A = Paimionlahti, B = Seili, and C= Utö. The red star indicates the location of the Seili ODAS monitoring station.
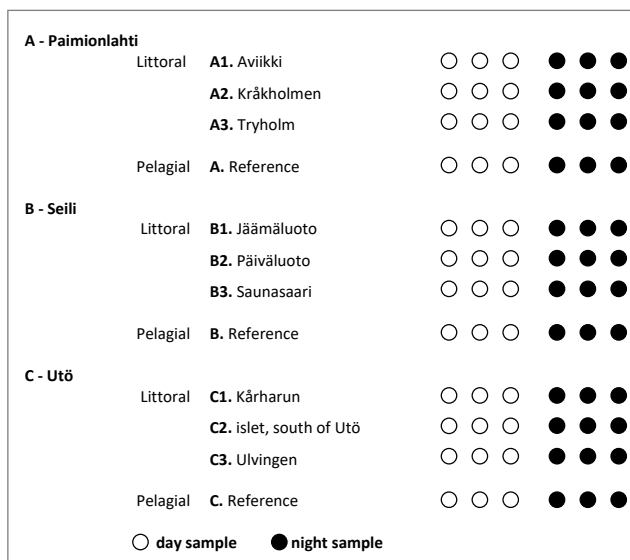
Mesozooplankton

According to, e.g., Vuorinen et al. (1998), Rajasilta & Vuorinen (2008), and Mäkinen et al. (2017), the dominant planktonic cladocerans in the study include the brackish water species *Bosmina longispina maritima* Leydig, the neritic genus *Podon* spp. (*P. polyphemoides* Leuckart, *P. leuckarti* Sars, *P. intermedius* Lilljeborg), *Evadne nordmanni* Loven, and *Cercopages pengoi* Ostroumov. In the innermost areas of the archipelago can also be found some freshwater species like *Daphnia* spp. (*D. cucullata* Sars, *D. christata* Sars), *Leptodora kindti* Focke, *Sida crystallina* Müller, and *Chydorus sphaericus* Müller). All cladocerans are prominent species in the above-thermocline plankton community and do not show any pronounced daily vertical migration through the thermocline (Purasjoki 1958, Burris 1980). Copepods common in surface layers belong to the order Calanoida and include *Acartia* spp. (mainly *A. bifilosa* Giesbrecht with *A. longiremis* Lilljeborg in deeper water and some *A. tonsa* Dana) and *Eurytemora affinis* Poppe. *Acartia* spp. and *Eurytemora* dominate the above-thermocline copepod biomass in the Archipelago Sea (Rajasilta & Vuorinen 2008) and generally in the Baltic Sea (Wasmund et al. 1996). Other less common species are *Limnocalanus macrurus* Sars, *Centropages hamatus* Lilljeborg, *Pseudocalanus acuspes* Giesbrecht, and *Temora longicornis* Müller (Rajasilta & Vuorinen 2008). The most abundant rotifer species in the Archipelago Sea belong to genera of *Keratella* spp. (*K. quadrata* Müller, *K. cochlearis* Gosse, *K. cruciformis* Thompson) and *Synchaeta* spp. (*S. baltica* Ehrenberg, *S. monopus* Plate, *S. curvata* Lie-Pettersen, *S. fennica* Rousselet), which are worldwide and common inhabitants in freshwater environments but are rarely found in brackish and marine habitats.

Zooplankton and hydrographical sampling

Zooplankton sampling was conducted during autumn 1997 in littoral habitats of three archipelago areas (Fig. 1). Here, we define a littoral site as a shore profile ranging from the shoreline to the outer edge of the belt of red algae, chiefly in depths of 10–15 meters. We studied only the rocky shores, which constitute the majority of possible habitat types at all of the locations studied. Area A represented the sheltered, inner archipelago in the Bay of Paimionlahti, area B was located in more open middle archipelago off the Island of Seili, and area D was situated in the outer archipelago in the vicinity of Utö island near the open sea.

Three replicate zooplankton samples were collected beyond the outer edge of Fucus belt from the depth of 1–2 m by using a tube sampler (Limnos-sampler, 3.6 l capacity). Reference samples were collected in a similar way in the open water areas (min depth $\geq$ 10 m) located between to the littoral sampling sites (Fig. 2). Samples were concentrated with a 50-μm plankton net mesh and stored in a buffered seawater-formalin solution (4%). In the laboratory, the zooplankton taxa were identified and analyzed according to protocols of HELCOM (1988). The copepods were identified into juveniles (N), copepodite stages of CI–CIII and CIV–CV, and adult stages of CVI (females / males). By contrast, only the adult stages of rotifers and cladocerans were analyzed.

► Figure 2. Chart of littoral/pelagic zooplankton sampling and seawater measurements at sampling sites.

At each littoral site, we measured the Secchi depth (m), temperature (°C), salinity (PSU), and oxygen content (mg/l) of seawater near the surface (0–1 m). More detailed information of the water sampling procedure in relation to zooplankton communities locally are presented in Hänninen et al. (2007).

Data and statistical analyses

As the data of littoral/pelagic sampling were not distributed normally, we applied non-parametric measures of heterogeneity, i.e., the Shannon-Wiener diversity index (H') and the Simpson index (D), for comparisons of biodiversity differences between the study sites. Both diversity indices describe α-diversity in the community, i.e., species numbers within a sample area (Crawley 1986). The Shannon-Wiener index is the most common index measuring the variability or information value of an ecological community. If the value of the index is higher, then there are more species in the community, and the species abundances in the community are more similar (Krebs 1999). The Simpson's Index D is the first non-parametric measure of diversity based on species dominance and abundance ratios, emphasizing the abundance of the most common species. It describes the likelihood that two individuals, randomly sampled from the community, will belong to different species. The Simpson index gets values between 0–1, with the higher the value, the greater the diversity (Simpson 1949).

Statistical analyzes were performed using the SAS statistical software version 9.0 (SAS Institute Inc. 1999). In the analysis, samples (A1–A3, B1–B3, etc.) within the sample sites were pooled to describe the species of the area in general. As the numbers of individuals of zooplankton species did not follow the Gaussian distribution even after transformations, we used again non-parametric tests instead of parametric tests. In comparison, we utilized the ANOVA corresponding Wilcoxon option of the SAS, which, depending on the levels of the classifying variable, automatically produce either a non-parametric Mann-Whitney U-test or a Kruskall-Wallis test depending on the level of depending variables. For possible trends and interrelationships observed in or between variables, we examined with GENMOD

(generalized linear models). GENMOD is an extension of traditional linear models that allows the mean of a population to depend on a linear predictor through a nonlinear link function and allows the response probability distribution to be any member of an exponential family of distributions. As criteria for the goodness of fit in GEN-MOD tests, we estimated with Deviance. The significance level for all analyses was defined as 0.05, i.e., a 95% confidence level (SAS Institute Inc. 1999).

In the analysis of species numbers, abundances, and diversity indices (H' and D), the formula was practically alike with all variables studied. First, we investigated, with the Wilcoxon option, whether there were general differences in the variables between the day and night, between the littoral and pelagic, or between regions A–C with all comparisons using a Mann-Whitney U test or Kruskall-Wallis test. Then, differences within regions were investigated correspondingly. Finally, for the variables, possible trends or interrelationships between different regions A–C were tested by GENMOD. Due to a few individuals, two samples were removed from area A, and therefore, the *n* in area A is smaller than the others. When necessary, the results were adjusted by Bonferroni correction (Sokal & Rohlf 1995).

In the analysis of community structures, the species were first divided into larger groups, i.e., rotifers, cladocerans, and copepods, in which relative percentages were examined in the littoral and pelagic areas between the day and the night. Then, species averages were regionally examined at different times of the day in the littoral and pelagic sites.

Results

Zooplankton proportions, abundances, and distributions

The study of relative abundances of the largest zooplankton groups revealed that rotifers had the highest prevalence both at littoral and pelagic habitats (Fig. 3, Table 1). The most species were found in the middle archipelago (11–17 species) and the outer archipelago (14–15 species). The lowest number of species was in the inner archipelago with 8–9 species (Fig. 4, Table 1).

In the littoral habitat, the number of species varied on average between 6 (area A) and 10 (area C). There were considerable variations in species numbers between areas, and a general trend was that numbers increased from the inner archipelago to the outer archipelagos (Fig. 4). The variation in species numbers in the littoral habitats of the inner and middle archipelagos were higher at night than during the day, being, however, the largest in the outer archipelago (Fig. 4).

In the pelagic habitats, the species numbers ranged from 7 (area A) to 11 (area C). Similarly, as in the littoral, species numbers differed significantly between areas and increased toward area C (Fig. 5).

The number of cladocerans were generally low in all areas. During the day, the proportion of cladocerans in the littoral community varied between 2–4% and between 2–8% at night (Fig. 3, Table 1). In the pelagic habitat, the respective proportions were between 0.7–3.3% during the day and 1–62% at night. The most common cladocera was *Bosmina longispina maritima*, which occurred in each area in the littoral and pe-

lagic habitats. In the inner archipelago, *B. longispina maritima* had an average of 1–4 individuals, and in the middle and outer archipelagos, a few dozen, being exceptionally high at night in the middle archipelago (area B), which changed the customary abundance pattern. The other, but rare, cladocerans found were *Cercopagis pengoi*, genus *Daphnia* sp., *Evadne nordmanni*, *Podon intermedius*, and *Pleopsis polyphemoides* in the middle and outer archipelago areas, and genus *Chydorus* spp. in the outer archipelago areas (Table 1).

The areal proportions of copepods in the littoral habitat ranged from 4% to 31% during the day and between 9% and 35% during the night (Fig. 3). In the pelagic habitat, the corresponding proportions of copepods varied between 2–26% and 3–26%, respectively. Relatively most copepods were found in the inner archipelago from where their numbers then decreased towards the outer archipelago. The most common copepod was *Acartia bifilosa*, which was present in each area (Table 2). In the littoral habitat, the amounts of *A. bifilosa* ranged between 20–123 individuals, and
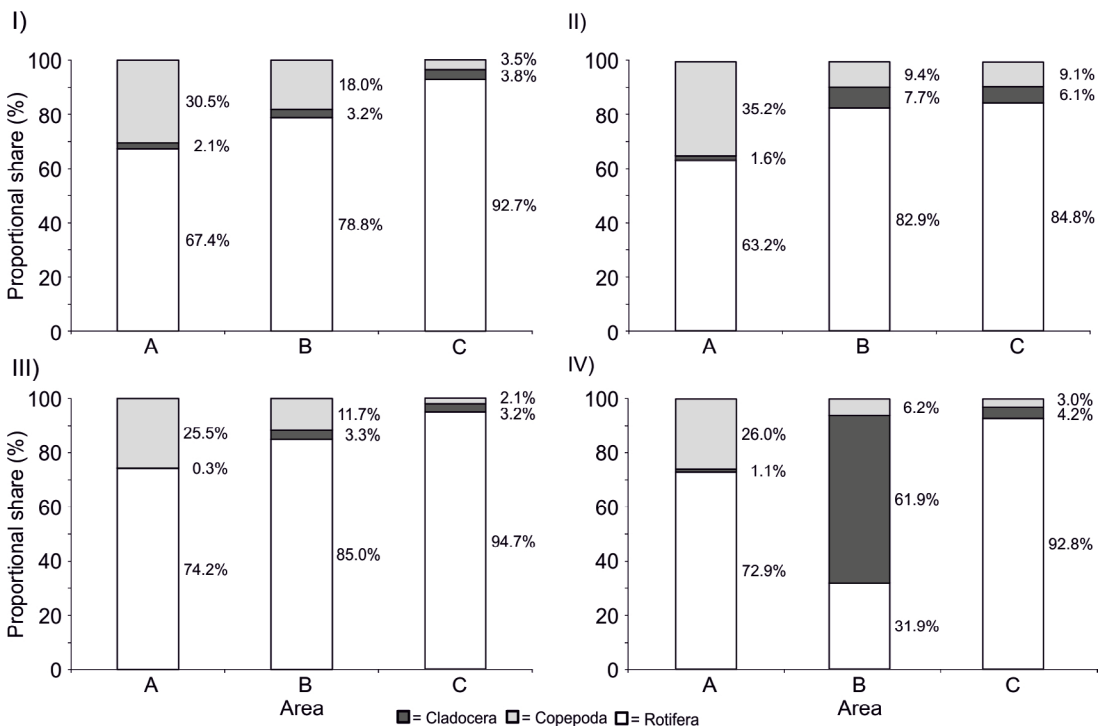

Figure 3. Relative proportions of cladocerans, copepods, and rotifers as a percentage (%) of total average numbers by study areas.
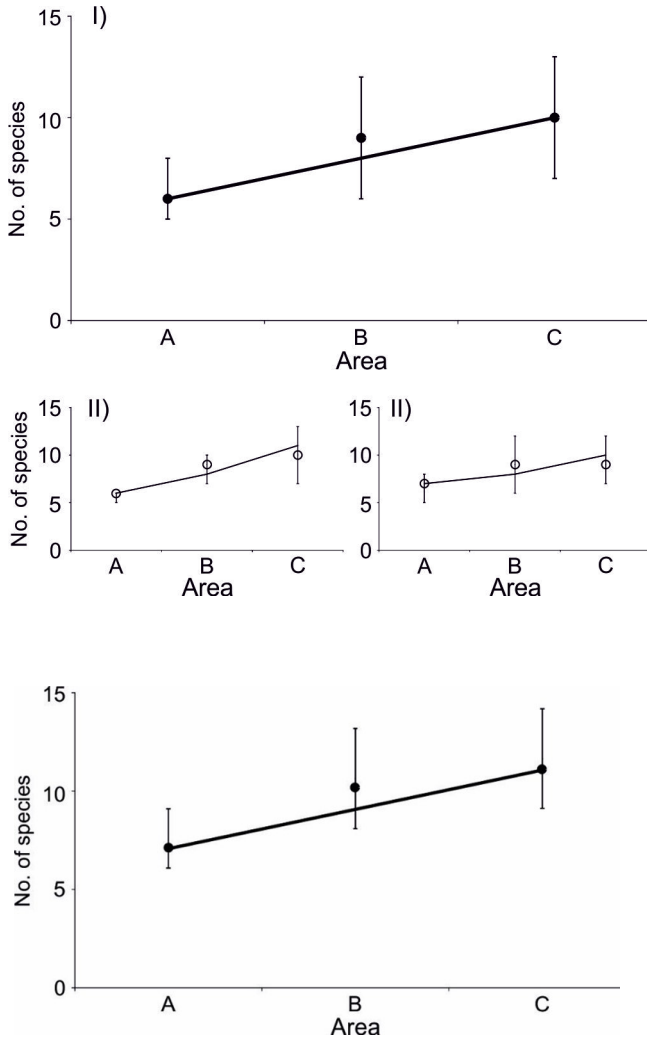
Figure 4. Littoral species numbers from area A to area C. The lines are based on the GENMOD prediction. Filled and open dots are mean averages with 95% confidence intervals. I) Pooled number of species: $\chi^2=14.66$, df=1, p=0.0001, n = 52; II) No. of species during the day: $\chi^2=12.11$, df=1, p=0.0005, n=27; and III) No. of species during the night: $\chi^2=3.49$, df=1, p=0.0618, n=25.

Figure 5. Pooled number of pelagial species from area A to area C based on the GENMOD prediction: $\chi^2=4.84$, df=1, p=0.0278, n=18. Descriptions as in Fig. 4.

in the pelagic habitat, between 19–168 individuals. *Eurytemora affinis* was evenly distributed with 2–10 individuals in each area. Also, *Temora longicornis* and *Cyclopoida* sp. were present in each area (mean 1–2 ind.), *Centropages hamatus* was present only in the outer archipelago, and *Pseudocalanus acuspes* in the middle archipelago (Table 1).

When observed by the time of the day in the littoral habitat, the proportion of rotifers at areas A–C varied between 67% and 93% during the day and between 63% and 85% during the night. The corresponding proportions for the pelagic habitat were between 74–95% and 32–93%, respectively (Fig. 3). In general, the relative pro-

portion of rotifers appeared to increase from the inner archipelago to the outer archipelago. The largest numbers of rotifers were found in genus *Keratella* (Table 1). The most abundant species in the study was *Keratella cochlearis*, which occurred in each region and whose species numbers ranged between 103–484 individuals in the littoral and 149–817 individuals in the pelagic. The second common rotifer species was the *Keratella quadrata*, which occurred in each area in both the littoral (16–122 individuals) and the pelagic (71–427 individuals) habitats. The largest numbers of individuals of *K. quadrata* were observed in the pelagic area of the outer archipelago. *Keratella cruciformis* was also abundant, mostly in

Table 1. Mean numbers of species in study areas at different times of the day, and the total number of species present in the area. A = inner archipelago, B = middle archipelago, C = outer archipelago, L = littoral, and P = pelagic areas.

Area		A		B		C	
Species		day	night	day	night	day	night
CLADOCERA							
Bosmina longispina maritima	L	4	3	10	36	23	11
	P	1	2	11	454	36	29
Daphnia sp.	L	-	3	1	3	-	-
	P	1	1	5	8	-	-
Cercopagis pengoi	L	-	-	1	2	-	-
	P	-	3	2	-	-	-
Pleopsis polyphemoides	L	-	-	-	2	4	7
	P	-	-	1	2	5	10
Podon intermedius	L	-	-	1	2	1	-
	P	-	-	-	-	2	1
Evadne nordmanni	L	-	-	-	1	3	1
	P	-	-	-	-	2	2
Chydorys sp.	L	-	-	-	-	-	1
	P	-	-	-	-	-	-
COPEPODA							
Acartia bifilosa	L	53	123	67	36	20	22
	P	168	136	63	39	19	24
Eurytemora affinis	L	2	2	3	10	5	4
	P	4	8	3	3	5	3
Temora longicornis	L	1	6	1	2	1	2
	P	1	1	-	-	2	-
Pseudocalanus acuspes	L	-	-	2	7	-	-
	P	-	-	-	4	-	-
Centropages hamatus	L	-	-	-	-	1	1
	P	-	-	1	-	1	2
Cyclopoida sp.	L	1	1	1	1	2	1
	P	1	-	1	-	2	1
ROTIFERA							
Keratella cochlearis	L	103	178	272	417	484	146
	P	374	314	385	149	817	465
Keratella cruciformis	L	7	11	4	3	62	36
	P	26	21	9	6	87	67
Keratella quadrata	L	16	18	40	63	212	91
	P	105	71	88	75	427	390
Synchaeta baltica	L	-	-	2	3	3	1
	P	-	-	2	4	2	2
Synchaeta monopus	L	-	-	4	6	3	2
	P	-	-	8	5	1	4
Synchaeta curvata	L	-	-	-	1	1	2
	P	-	-	-	-	-	1
Filinia longiseta	L	-	-	1	-	-	-
	P	-	-	-	-	-	-
Tot no. of species	L	8	9	15	17	15	15
	P	9	9	13	11	14	14

Table 2. The mean number of developmental stages of copepod species in study areas at different times of the day. A = inner archipelago, B = middle archipelago, C = outer archipelago, L = littoral, P = pelagic, CIV–V = copepodite stages IV–V, CI–III = copepodite stages I–III, N = nauplius larvae.

Area			A		B		C	
Species	Hab.	Stage	day	night	day	night	day	night
Acartia bifilosa	L	CIV–V	2	1	1	10	16	44
	L	CI–CIII	16	19	1	1	20	32
	L	N	155	304	176	83	41	13
	P	CIV–V	1	-	4	5	6	16
	P	CI–CIII	17	17	3	7	19	23
	P	N	597	389	260	153	51	61
Eurytemora affinis	L	CIV–V	-	-	-	2	3	4
	L	CI–CIII	-	-	-	-	7	3
	L	N	2	2	3	12	6	4
	P	CIV–V	-	-	-	-	2	2
	P	CI–CIII	-	-	-	1	3	-
	P	N	5	8	4	-	9	4
Temora longicornis	L	N	-	2	-	-	1	1
	P	N	1	-	-	-	1	-
Pseudocalanus acuspes	L	N	-	-	-	1	-	-
	P	N	-	-	-	1	-	-
Centropages hamatus	L	N	-	-	-	-	-	-
	P	N	-	-	-	-	-	1
Cyclopoida sp.	L	CI–CIII	-	-	-	-	1	1
	L	N	-	-	-	-	1	-
	P	CI–CIII	-	-	-	-	1	-
	P	N	-	-	-	-	1	-

the outer archipelago (Table 1). Besides *Keratella* rotifers, a few members of the *Synchaeta* genus were found from the intermediate and outer archipelagos (Table 1).

Developmental stages of zooplankton

Developmental stages of nauplius larvae and copepodite stages I–III and IV–V, were determined for all copepod species. The only species in which individuals were found for all five classes were *A. bifilosa* and *E. affinis* (Table 2). *Acartia bifilosa* was present in each area with the highest number of stages in the inner archipelago in both the littoral and pelagic habitats (Fig. 3). In the littoral habitats, individuals in the inner archipelago accounted for about half (57 ind.) of the number of pelagic individuals (102 ind.). In both cases, the numbers of *A. bifilosa* decreased from the inner archipelago toward the outer archipelago (Fig. 3).

The variation in occurrence was large in both the littoral and pelagic habitats, especially in the inner archipelago. In general, the numbers of individuals in the littoral and pelagic did not differ significantly, although there were on average more individuals in the pelagic habitat. Between night and day, the numbers of individuals in each habitat did not differ statistically (Fig. 3).

E. affinis nauplii were found in the littoral and pelagic habitats with on average 2 to 12 individuals in each area and at each time of day, except in the inner archipelago. During the pelagic night, no individuals were observed (Table 1). Copepodite stages I–III and IV–V were observed mainly in the outer archipelago and occasionally in the middle archipelago at night. No copepodites of *E. affinisis* were observed in the inner archipelago (Table 2).

Of the other species, only specimens of the nauplius stages were randomly found, but the occurrences were always very rare, as one nauplii larvae was found for *C. hamatus*, *Cyclopoida* sp., *P. acuspes*, and *T. longicornis*. For *Cyclopoida* sp., an average of one copepodite I–III was observed in the outer archipelago (Table 2).

Diversity differences

Littoral habitats

Among littoral study areas, the Shannon-Wiener diversity index H' varied between 1.32–2.09 and the Simpson index D between 0.50–0.69 (Fig. 6). The areal difference in littoral diversity was statistically significant for both indices (H': $\chi^2=35.43$, df=2, p=0. 0001, n=52; D: $\chi^2=24.45$, df=2, p=0.0001, n=25; Kruskall-Wallis test). Moreover, in littoral habitats, both diversity indices increased towards the outer archipelago (Fig. 4). The Simpson Index D differed only in the outer archipelago, where the night diversity index was the highest (D: $\chi^2=6.79$, df=1, p= 0.0091, n=25; Kruskall-Wallis test).

Pelagic habitats

In pelagic areas, Shannon-Wiener H' values were between 1.55–1.82, and the Simpson's D values between 0.59–0.63. In general, the pelagic H' diversity varied significantly among the study areas ($\chi^2=1.42$, df=2, p=0.0033, n=18, Kruskall-Wallis test), but no such differences were found for the D index. The H' diversity did not differ between day and night, but the Bonferroni-adjusted D index showed a statistical difference ($\chi^2=5.48$, df=1, p=0.0193, n=18, Mann-Whitney U-test) revealing that the night had on average higher values than during the day. In pelagic study areas, there were no clear trends toward the outer archipelago for either index (Fig. 6).

Littoral versus pelagic habitats

In general, we found that pelagic diversities for both indices in study sites showed significantly higher values than littoral ones (Fig. 7, Table 3). In pelagic habitats, diversities were high in the inner and middle archipelagos, but however, in the outer archipelago, those were higher in the littoral habitats. Also, the variation in the littoral diversities was generally greater than that of the pelagic (Fig. 7).

The study also showed that, in each area at night, diversities differed significantly between littoral and pelagic habitats (Table 3). As a rule, in the littoral habitats, values were typically lower at night in the inner and middle archipelagos and higher in the outer archipelago than in the pelagic habitats. During the day, as a rule, littoral and pelagic diversities did not differ in the areas (Table 3).
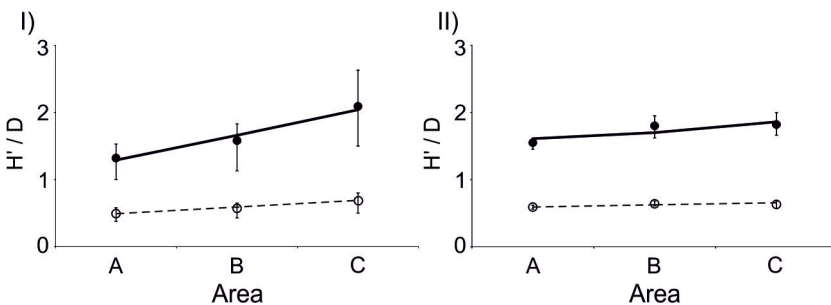

Figure 6. Diversity indices for I) littoral and II) pelagic habitats from A to C areas. The lines are predicted by the GENMOD generalized linear model. Filled and open dots are mean averages with 95% confidence intervals. The solid lines described Shannon-Wiener H' indices and the dashed lines Simpson Diversity D indices.
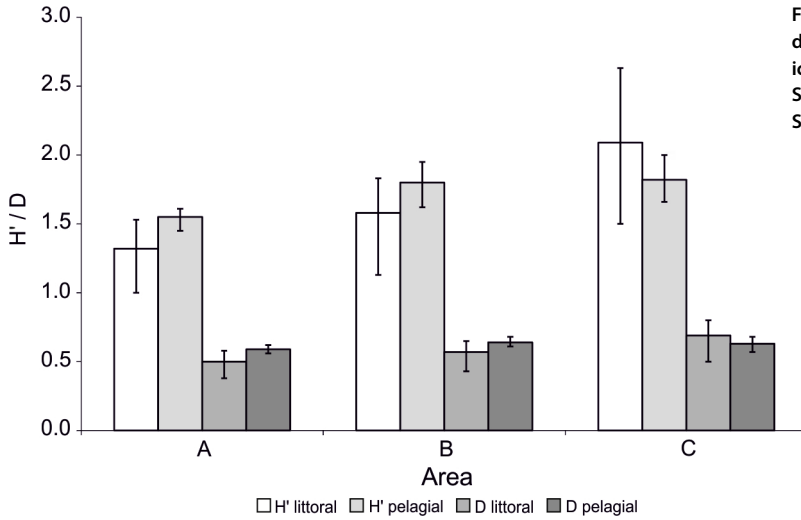
Figure 7. Mean values and 95% confidence intervals of littoral and pelagic diversity indices comparisons. H' = Shannon-Wiener Diversity Index, D = Simpson Diversity Index.

Table 3. Comparison of littoral and pelagic diversities H' and D by region and day and night separately. Mann-Whitney U-test. p = day, y = night.

Index	Area	Day (d) / Night (n)	df	χ^2	p	Mean	
						littoral	pelagial
H'	A		1	10.05	**0.0015**	1.32	1.55
	A	d	1	2.47	0.1160	1.40	1.50
	A	n	1	5.73	**0.0167**	1.23	1.59
	B		1	6.42	**0.0113**	1.58	1.80
	B	d	1	0.69	0.4054	1.59	1.73
	B	n	1	6.23	**0.0126**	1.57	1.87
	C		1	5.14	**0.0234**	2.09	1.83
	C	d	1	1.03	0.3095	1.89	1.71
	C	n	1	5.34	**0.0208**	2.29	1.94
D	A		1	10.05	**0.0015**	0.50	0.60
	A	d	1	3.09	0.0790	0.54	0.58
	A	n	1	5.73	**0.0167**	0.46	0.61
	B		1	5.44	**0.0196**	0.57	0.64
	B	d	1	0.69	0.4054	0.58	0.62
	B	n	1	4.52	**0.0335**	0.56	0.65
	C		1	4.27	**0.0388**	0.69	0.63
	C	d	1	0.69	0.4054	0.63	0.59
	C	n	1	6.23	**0.0126**	0.74	0.67

Discussion

Study revealed that the archipelago zones can, to a certain extent, be observed on the basis of the numbers of zooplankton species. Although there were variations in species numbers between areas, the general trend in the study was that species numbers had higher values when moved from the inner archipelago towards the outer archipelago in both the littoral and pelagic habitats. Most of the species in the zooplankton community were found in the outer archipelago. This agrees with various earlier studies that, in general, the species number increases when we enter from sheltered, less salty shoreline waters to the more open marine environment (Leppäkoski et al. 1999, Hänninen & Vuorinen 2001, Bonsdorff et al. 2003, O'Brien et al. 2003, Hänninen et al. 2007). The lower salinity near the mainland is due to the freshwater river runoffs from the catchment area

and salinity level increases from the inner archipelago (about 5.5 PSU) towards the outer areas (about 6.5 PSU) (Hällfors et al. 1981, Leppäranta & Myrberg 2009). This explains also the increase in the number of zooplankton species towards the outer archipelago, as salinity regulates most the composition of the zooplankton community (Hänninen 1999, Leppäkoski et al. 1999).

The study reflected the zooplankton compositions and distributions that have been reported in numerous previous surveys – the species number were low in every respect (e.g., Ojaveer et al. 1998, Vuorinen et al. 1998, Dippner et al. 2000, Möllmann et al. 2000, Kornilovs et al. 2001, Möllmann & Köster 2002, Hänninen et al. 2003, Vuorinen et al. 2003, Mäkinen et al. 2017). On one hand, the species scarcity in the study is understandable, as it reflects the small number of zooplankton species in the Baltic Sea in general. On the other hand, it can also be considered that, in the case of the Archipelago Sea, the terms of "pelagial" and "littoral" are more or less mixed, as locally, there is no clear continuum from the shoreline to the open sea area due to shallow water and numerous islands relatively close to each other. Thus, finding this continuum is ultimately a question of scale and therefore not always obvious. Nevertheless, more biota and a higher number of species are expected near the coastal zone than in the open water (Segerstråle 1953, 1969). In the littoral habitat, the complex and multidimensional environment with a benthic flora and algae create a place for species reproduction, protection, and growth as well as a nursery area for most of the brackish water animals in the Baltic Sea (Voipio 1981). Therefore, the littoral habitat is considered to be the most diverse ecosystem in the Baltic Sea (Leppäkoski et al. 1999). Respectively, the pelagic water area forms its own independently functioning ecosystem, in which organisms receive food mostly from the organic materials in seawater that is based either on the phytoplankton's primary production or other heterotrophic organisms. The photic, or productive upper layer in the sea, reaches as far as there is enough light energy, typically to the depth of 15–20 meters. This layer is estimated to produce almost 90% of all organic production in the pelagic of the seas (Krebs 1999). But as mentioned above, the change between ecosystems functioning in the shallow sea could sometimes be difficult to distinguish.

We also found a general increasing trend for both diversity indices H' or D from the inner archipelago to the outer archipelago either in the littoral and pelagic habitats. In the littoral habitat, both indices increased constantly towards the outer archipelago, but in the pelagic habitats, the highest values were found in the middle areas from where we found the highest species number as well. The middle archipelago has also been found to have higher diversity than other areas of the archipelago in terms of benthic fauna (O'Brien et al. 2003) and plant communities (von Numers & van der Maarel 1998).

We were also able to show manifestations of migration patterns in our study. In day-to-night diversity comparisons, littoral H' and D indices were high in the inner archipelago during the day, but at night, in the middle and outer archipelagos. Similarly, our findings of species abundances in the littoral habitat indicated that, during the day, there are fewer individuals in the surface water in the inner archipelago, but there the abundances increased at night. This revealed that zooplankton masses migrate to the surface as the sun sets, which follows the concept of "Normal diel vertical migration" (e.g., Cohen & Forward 2002).

As the sun sets in the evening, zooplankton launch their migration towards their night residence, the sea surface layer. Respectively, in the morning, as the amount of light increases at sunrise, they migrate back to the deeper water layers to the depth of optimal light conditions for each species (Nybakken 1997). The migration depth or distance of a single individual or species is influenced by the movements of the water masses, gravity, wind, rain, temperature, pressure, pH, or oxygen content of the sea water and the individual's swimming ability. By migrating, an individual aims to reach a level where its living conditions are most favorable (Clarke 1934, Ackefors 1969, Hällfors et al. 1981). Numerous explanations have been suggested to account for why zooplankton migrate. The most common explanation is that species move deeper to dimmer layers to avoid visually oriented predating animals such as birds or fish (McLaren 1963, Vuorinen 1986, Lampert 1993). Predation is a major factor influencing the zooplankton community struc-

ture (Brooks & Dodson 1965). It has also been reported that, by migrating, species tend to avoid damage due to too intensive solar radiation (Nybakken 1997) or because migration helps to move also horizontally with currents (Hardy 1953). Migration could also save energy because vital functions in deeper, colder water are slowed down (McLaren 1974, McAllister 1969).

In the present study, the littoral diversity at the study areas differed from the pelagic only at night. In the inner and middle archipelagos, pelagic diversity at night was higher than in the littoral, whereas, in the outer archipelago, a greater diversity was found in the littoral habitat. This reveals that, in the more sheltered inner and middle archipelagos, individuals swim to the surface at night following the "Normal diel vertical migration" stated by Cohen & Forward (2002) and prefer to forage in more open water in the pelagic habitats. In contrast, in the outer archipelago, there were more individuals in the littoral habitats at the same time. Such horizontal migration of zooplankton between day and night, called the "Reverse diel vertical migration" (Ohman et al. 1983), can be largely explained by the same reasons that were presented earlier for the vertical migration in the two innermost areas. Probably, the most likely explanation is that predation varies in the different parts of the archipelago. In the inner archipelago, zooplankton migrate to the surface at night to graze phytoplankton and to avoid predators, mainly visually hunting fish ("Normal diel vertical migration"), and, during the day, they sink deeper into the protection of vegetation and algae. An important zone for maintaining vegetation and diversity in the middle archipelago, and especially in the windy and wavy outer archipelago, is the zone of *Fucus* algae. A large number of animal species in the Baltic Sea live in the shelters of Bladderwrack (*Fucus vesiculosus* L.) or use it as for food or nesting area (e.g., Barboza et al. 2019). In the outer archipelago, zooplankton lies at the surface during the day when the case is reversed migration ("Reverse diel vertical migration", Ohman et al. 1983). The reverse migration of zooplankton could occur by means of avoiding those predators that migrate together with them following the same migration patterns. The predators may be, for example, other zooplankton or invertebrates that avoid their own

predators by roaming (Lampert 1989). However, the pattern of migration varies by species (Cohen & Forward 2002), and some species do not migrate at all.

The number of cladocerans were generally low in all areas, and there were no significant differences in their numbers between habitats or in the time of day. Due to the low salinity in the Archipelago Sea, it is understandable that the origin for the most prevailing species is freshwater. Accordingly, the most common cladocera was *Bosmina longispina maritima* which, as can be concluded from the specific epithet, manage well also in low salinities occurring evenly in each area, both in the littoral and pelagic habitats. The exceptionally high proportion, 62%, of cladocerans at night in the middle archipelago (area B) can be explained by the exceptionally high patch of *Bosmina longispina maritima* in the area and in all samples with more than 400 individuals, which accounted for 61% of all cladocerans species showing a disruption in the customary abundance pattern.

The copepods showed slightly lesser abundances during the day than at night in the littoral habitat, but, in the pelagic habitat, such a change was not evident. The most copepods were found in the inner archipelago, from where their numbers decreased towards the outer archipelago. This was generally the case also for the developmental stages of copepods, as well. The most common copepod species were *Acartia bifilosa* and *Eurytemora affinis*, which is in accordance with the general abundance pattern existing in the Baltic Sea (e.g., Vuorinen et al. 1998). It is also known that the older stages of development of *E. affinisis* are deeper than the younger ones (Ackefors 1969). Practically, the rest of the copepod species favors a higher salinity content in the seawater, which explains their scaritines in the samples. Typically, those species are more common in the central and southern Baltic Sea, where the salinity is higher due to the high saline seawater supply from the North Sea (e.g., Hänninen et al. 2015, Hänninen 2022).

The abundances of rotifers indicated an inverse of distribution patterns compared to copepods, as their proportions appeared to increase from the inner archipelago to the outer archipelago. Moreover, the diel distribution showed also

an opposite pattern against the copepods as, at night, the rotifer abundances were decreased in the pelagial habitats but increased in the littoral habitats. This indicated a kind of small-scale horizontal migration or drift from the pelagial habitat nearer to the shallow shoreline. The largest numbers of rotifers belong to genus *Keratella* spp., which is also the most common rotifer group in the Baltic Sea, as well (e.g., Vuorinen et al. 1998).

The sampling for this study was conducted in 1997, but in light of the known zooplankton changes in the archipelago area, it could be argued that the observed general trends and patterns between archipelago zones and littoral-pelagic areas could hold true even today. According to monitoring data collected in the middle archipelago during 1967–2013, since the 1960s, the zooplankton community composition in the Archipelago Sea has been mainly affected by the large-scale decreasing trend in surface water salinity and, to some extent, by the observed temperature increase as well (Mäkinen et al. 2017, Hänninen 2022). In their study, Mäkinen et al. (2017) found that large-sized and marine taxa, having narrower tolerance limits, had responded to the large-scale changes with an overall decrease in their abundance, which was most apparent during the 1980–1990s. On the contrary, the dominating species, such as *A. bifilosa*, *E. affinis*, and *B. longispina maritima*, which exhibit a wider tolerance to salinity and temperature variation, did not show any major trends in abundance, albeit some species-specific and inter-annual variation was evident. Based on this information, no major shifts in abundance or diversity, at least for the most dominant taxa, could be expected to have happened since the 2000s, albeit some interannual variation would have likely emerged if the sampling of this study had continued for several years. The previous is likely true, at least, for adult and larger zooplankton species, but it should be noted that no quantitative knowledge of the long-term variation of small-sized species or life-stages currently exists as most monitoring data, such as that used by Mäkinen et al. (2017), are based on samples collected from a pelagic station with a 150-μm net. In addition, little information is available, locally, about how eutrophication, pollution, and invasive species, i.e., factors that are known to reduce diversity, have influenced zooplankton in the archipelago region. In the Neva estuary, Telesh (2004) found that the Shannon index H' of zooplankton decreased by more than a third in the most contaminated areas. She also found that the Shannon index calculated from zooplankton clearly describes the ecological status of the Neva estuary. Similarly, the lowest diversity indices in the present study were found mainly in the innermost study area, near the coast.

This current study adds to the existing knowledge of species variation and diversity within the archipelago area, thereby improving our understanding on how species may respond to environmental changes locally and how these changes may be reflected within the food web. Accordingly, zooplankton represent a good study target, as they are the main food for many pelagic fish and fish larvae (Kornilovs et al. 2001). Presently, within the Archipelago Sea, small zooplankton species, such as *A. bifilosa*, *E. affinis*, and *B. maritima* seem to construct the bulk of the available zooplankton food available for planktivores such as Baltic herring (*Clupea harengus membras* L.) and sprat (*Sprattus sprattus* L.). The significance of the observed patterns to the planktivore diet is unclear, but it may have some significance for fish larvae and local populations that do not migrate out of the archipelago to areas where zooplankton taxa with higher nutritional value are more abundant.

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